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OSCILLATIONS IN THE VISUAL RESPONSE TO PULSED STIMULI

By

Franklin F. Holly

SENSORY RESEARCH DIVISION

Visual Science Group

June 1982

U.S. ARMY AEROMEDICAL RESEARCH LABORATORY
FORT RUCKER, ALABAMA 36362

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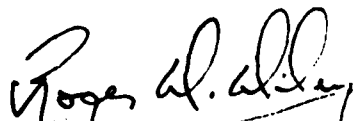
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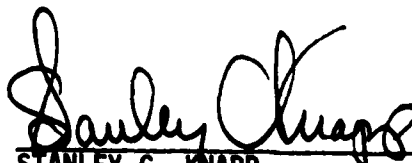
Reviewed:

Bruce C. Leibrecht, Ph D., MAJ, MSC
Director, Sensory Research Division

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20. ABSTRACT:

Dunlap (1915) reported a phenomenon in which a single photic pulse, pre-
sented in the periphery under mesopic conditions, is perceived as two sequential
flashes. The present work indicates that this double-flash effect is but a
special case of a class of auto-oscillatory phenomena occurring at a frequency
in the neighborhood of 10 Hz. Flicker studies by several investigators (e.g.,
de Lange, 1958) have indicated a resonance (temporal MTF peak) at approximately
10 Hz. It is believed that the frequency of the oscillatory phenomena described
here results from the natural frequency of the network responsible for this
peak. It is also believed that these phenomena are related to the oscillatory
potentials which have been recorded from retina and cortex.

The impetus for this work was provided by the need to explicate certain
oscillatory phenomena which had been noted in the course of evaluating proposed
lighting systems on new Army helicopters.

ACKNOWLEDGEMENTS

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INTRODUCTION

The latest generation of Army helicopters incorporates several new lighting techniques. The formation lights consist of electroluminescent panels powered by 110 volts and cycling at a rate of 400 Hz. The anti-collision lighting system utilizes xenon strobe lights which emit an approximately 100 μsec pulse at a rate of approximately 1 per second. In the course of evaluating these new techniques, a strange oscillatory phenomenon was noted. At most distances, when the observer is in a mesopic adaptational state and when the light from an electroluminescent panel is swept across the retina by a saccadic eye movement the single panel actually appears to be a string of panels. This is not surprising when it is remembered that the electroluminescent panel is actually pulsing at a rate of 400 Hz and when the velocity of retinal displacement is calculated relative to this pulsing frequency. That is, each pulse occurs at a slightly different place on the retina thus producing this series of images. What is surprising, however, is that this string of images itself appears to pulse two or three times before disappearing. Also, at mesopic adaptational levels when the reflection from the xenon strobe lights is viewed in the periphery with the eyes either stationary or moving the single pulse often appears to be a series of two or three pulses with each succeeding pulse usually weaker than the previous one. That is, what is actually a single pulse appears to be a series of damped oscillations. It has even been reported that some anticollision lights have been needlessly replaced because they were erroneously thought to be emitting multiple pulses. It was decided to investigate these strange effects in the literature and in the laboratory in order to determine under just what conditions they can be expected to occur.

Dunlap (1915) reported a phenomenon in which a single photic pulse, presented in the periphery under mesopic conditions, is perceived as two sequential flashes. Bartley and Wilkinson (1953) emphasized that this effect occurs under conditions in which two populations of photo-receptors, each having a different latency, are responding. They believed however, that it is incorrect to simply say that the first response is that of the shorter-latency photoreceptors (cones) and the second response is that of the longer-latency photoreceptors (rods). Rather, they be-lieved the effect to be some sort of genuine after-activity resulting from interaction between the two systems. Springer, Deutsch, and Stanley (1975), using two real pulses, found that an interval of 104 msec between these pulses was required in order to match the perceived interval in the double-flash effect.

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The present work indicates that this double-flash effect is but a special case of a class of auto-oscillatory* phenomena occurring at a frequency in the neighborhood of 10 Hz. That is, although the two-population case certainly produces the strongest auto-oscillation, purely cone-generated and purely rod-generated oscillations can be produced under some conditions. Furthermore, more than two oscillations can often be seen regardless of whether both rods and cones or only a single population is responding.**

By using a forcing function (flicker stimulus) and examining the complete response (forced response + natural response), a number of investigators (e.g., de Lange, 1958) have shown a resonance (temporal MTF peak) at approximately 10 Hz indicating a natural response of this frequency. The exact frequency of the peak depends upon the background luminance. It is believed that the frequency of the auto-oscillations described here results from the natural frequency of the network responsible for this peak.

In the work to be described, these oscillations were documented by means of a matching technique in which single photic pulses varying in intensity, chromaticity, size, and retinal locus were presented to the observers' left eye which was held in various states of adaptation. His task was to construct a waveform of real-light oscillations (presented to the right eye) which matched the apparent oscillations generated by the single pulses. In other parts of this work, it was shown that: 1) these auto-oscillations affect the increment threshold only minimally

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* In this psychophysical work, the term auto-oscillation will refer to all oscillations subsequent to the first one (all perceived oscillations in the absence of photic oscillations). This effect can be easily demonstrated to someone who is adapted to normal room illumination by bringing him into a totally dark room and then, before he dark adapts, presenting a < 50 msec light pulse with the instructions to look a few degrees off to the side. For demonstration purposes, I use a tachistoscope to present a 2^0, 19 photopic fL, white (fluorescent), 1.7 msec pulse. Although I introduce it as the "double-flash effect," observers often volunteer the information that they actually see more than just two flashes. Some of the subjects of Springer, Deutsch, and Stanley also reported "additional flicker," rather than simply a second flash.

** The possibility that these oscillations are artifacts produced by the stimulus was, of course, eliminated by means of a photocell. Moreover, the same auto-oscillatory responses have been produced using a number of different sources, e.g., tachistoscopic (fluorescent), xenon tube, glow modulator, and tungsten-halogen with electromechanical shutter.

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and 2) an equivalent background is not equivalent insofar as the auto-oscillations are concerned.

METHOD

OBSERVERS

The observers were the author and an assistant. Both have acuity correctable to 20/20.

APPARATUS

The apparatus (Figure 1) consisted of a Maxwellian view system in which two channels were directed to the left eye and two channels to the right eye. Tungsten-halogen bulbs were used as sources in each of the
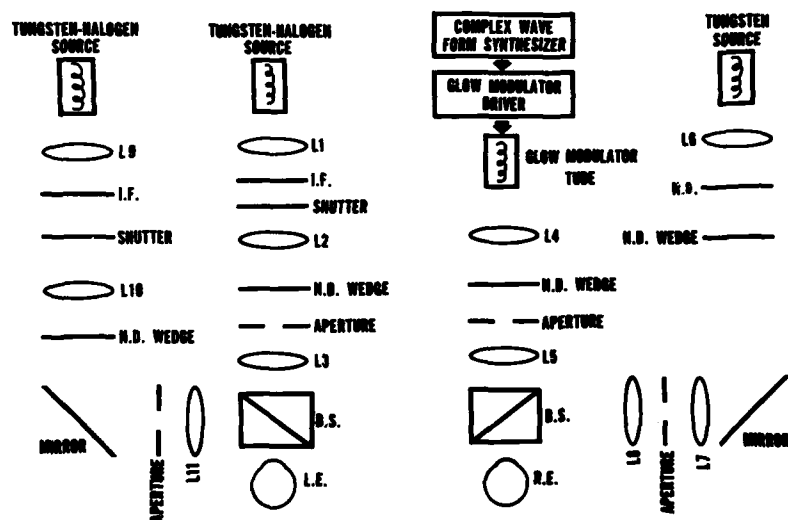
FIGURE 1. Diagram of the apparatus.

left channels. The source for one of the right channels was a glow modulator tube driven by a power amplifier which was in turn controlled by an Exact Electronics, Inc. Model 220* complex waveform synthesizer. This complex waveform synthesizer provided the observer with 40 individually adjustable knobs each of which controlled one "piece" of the waveform. Thus, the observer could construct a waveform of any shape to a resolution of the period ÷ 40. The other right eye channel had a tungsten source. Each of the left channels had Vincent Associates Model 200-1** electromechanical shutters which were controlled by Tektronix Model PG 505*** pulse generators. In the case where pulses were presented in both left channels (increment threshold work), a Tektronix FG 502*** *function* generator and a Tektronix DC 505*** counter-timer were added to coordinate the two shutters. This function generator provided a ramp which was fed to the two pulse generators and the interval between the pulses was determined by varying the trigger levels of the pulse generators. The intervals were set by means of the counter-timer. An integrating sphere with one section removed and neutral density filters were used to provide various pre-adaptation levels in some of the experiments.

PROCEDURE

Matching Experiments (No Background)

The various adaptation levels were produced by means of long tungsten exposures from the integrating sphere. The rod bleaching levels were calculated from the Alpern (1971) rhodopsin kinetic equation:

$$p = P + (p_0 - P)\ e^{-t/t_0 P}$$

where p = fraction of rhodopsin,

t = bleaching/regeneration time in seconds,

t_0 = 400 seconds,

p_0 = p when t = 0,

$P = I_0/(I + I_0)$,

I = retinal illuminance in scotopic trolands,

and $I_0 = 10^{4.4}$.

In one adaptation regimen, the left eye was dark adapted for 45 minutes. In a second adaptation regimen, the left eye was exposed to 8,000 scotopic trolands of illuminant C (correlated color temperature of approximately 6740^0k) for 15 minutes producing a 23% rhodopsin bleach. This color temperature was achieved by placing a daylight correcting filter over the tungston sources. For all other exposures, the tungsten sources were unfiltered except by neutral density filters. In a third adaptation regimen, the left eye was exposed to 14,000 scotopic trolands for 11 minutes producing a 33% rhodopsin bleach. In a fourth regimen, the left eye was exposed to 14,000 scotopic trolands for 11 minutes and then dark adapted for 11 minutes producing a 7% rhodopsin bleach. More-over, since preliminary work showed that not only the level of bleach but also the recency of bleach was important, a second 7% bleach of the left eye was produced by a different adaptation regimen: 5 minutes ex-posure to 3,700 scotopic trolands and then 1 minute of dark adaptation. These two 7% bleaches, produced by two different adaptation regimens, can be called metameric bleaches and were used to find the effects of recency by controlling, i.e., holding constant, the bleaching level. This latter 7% bleach will be referred to as the recent 7% bleach and the former 7% bleach will be called the old 7% bleach.

The right eye, on the other hand, was always bleached to the same 18% bleach level. This differential adaptation between the two eyes was achieved by occluding or placing an N.D. filter over one eye or the other, as necessary, for a given adaptation regimen so that the right eye was always exposed to 14,000 scotopic trolands for the final 3 minutes of the adaptation regimen. For example, in the 33% left eye bleach condi-tion, after both eyes were fully dark adapted, the left eye was exposed to 14,000 scotopic trolands for 11 minutes while the right eye was occluded for the first 8 minutes and then exposed to the 14,000 scotopic trolands for 3 minutes. In one of the 7% bleach conditions, after both eyes were fully dark adapted the left eye was exposed to 14,000 scotopic trolands for 11 minutes while the right eye was occluded. Then both eyes re-mained in the dark for 8 minutes, and finally, the left eye was occluded while the right eye was exposed to 14,000 scotopic trolands for 3 minutes.

Immediately after each adaptation the observer assumed his position in the Maxwellian view apparatus and three single 35 msec pulses, de-livered 3 seconds apart, were presented to the test (left) eye with no background. Then, with central viewing of the 1^0 matching field pre-sented to the right eye, he attempted to construct from memory a wave-form which matched the perceived waveform of the test pulse. He per-formed this by adjusting the knobs on the complex waveform synthesizer. In most cases, square pulses were used in the matching waveform. The shape of the pulses was irrelevant since the duration used was below the visual system's integration time and square pulses were easier to use. After constructing a waveform, he viewed it, made modifications to it in an attempt to achieve a closer approximation, and then viewed it once

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more. Then the entire adaptation, test, and matching procedure were repeated. These procedures, usually extending over several sessions, were repeated until the observer was satisfied that he had made as good a match as possible. When four such satisfactory matches had been made, the whole procedure was repeated for the next stimulus-adaptation condition. The other right eye channel presented an 8^0, white, 34 photopic trolands, steady background to the matching field. The background was used because it either greatly diminished or eliminated the auto-oscillations. This was desirable in order that the auto-oscillation effect itself not be confounded with the attempt to measure it.

The test flashes were of four different chromaticities. These were produced by Baird-Atomic interference filters* peaking at 460, 555, 620, and 680 nm. The intensities ranged from .023 to 2,000 photopic trolands and from .032 to 560 scotopic trolands. All targets were homogeneous circular discs. Targets of $\frac{1}{2}^0$ were centrally fixated and those of $1\frac{1}{2}^0$ were presented 2, 5, and 8^0 from the fovea. The fixation light was a small red point source but it was found that the oscillations were stronger if the observers did not actually fixate this light. Rather, they were instructed to look slightly off to one side or the other. For the centrally viewed targets, the fixation light was deliberately placed slightly to the left of the test field center and the observers directed their gaze just to the right of this light.**

Matching Experiments (Equivalent Background)

In these experiments the test flash had an intensity of four photopic trolands, a duration of 35 msec, and peaked at 460 nm. The other left channel was used to present a steady 7^0 white background which constituted an equivalent (8 scotopic trolands) background to the recent 7% rhodopsin bleach condition. This equivalent background level was determined in the usual manner by first finding the no-background threshold with the eye at a 7% recent bleach and then determining the background level required to produce this same threshold with the eye fully dark adapted. In one condition, the test flash was presented 2 seconds after the onset of the background and in the other condition it was presented

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* Baird-Atomic, Inc., 125 Middlesex Turnpike, Bedford, MA 01730
** Fixation may introduce an attentional factor which tends to interfere with peripheral perception. Cobb and Dawson (1960) reported changes in the occipital VER when the subject fixates a small detail in the visual field.

60 seconds after the onset of the background. Matches were again made with the waveform synthesizer-glow modulator system.

Increment Threshold Experiments

In these experiments, an attempt was made to map out the auto-oscillations by means of an increment threshold probe. A $\frac{1}{2}^0$ diameter circular (disc) probe of 10 msec duration and peaking at 560 nm was presented at various intervals from 140 msec before to 400 msec after the flash, which had a duration of 35 msec. Observers determined the thresholds for the probe by adjusting a neutral density wedge in the probe channel (ascending trials only). The chromaticity-intensity-adaptation combination selected for the test flash was one which produced strong auto-oscillation, i.e., its chromaticity peaked at 555 nm, it produced a retinal illuminance of 200 photopic trolands, and it was presented with the eye held at a 7% (recent) bleach. The flashes were presented 3^0 from the fovea.

RESULTS

MATCHING EXPERIMENTS (NO BACKGROUND)

A full set of data are reported for subject FH. Except where specified, the data reported are typical in that the number of oscillations nearly always fell within plus or minus one of the number shown. The data from subject VR are similar and some of his data are also presented. In some of the strong two-population oscillations, there was considerable within-subject variability in the temporal spacing of the matching pulses and this is shown by the dotted lines. The amplitude variability of some of the matching pulses is shown by the dashed lines.

It is important to note that although under some conditions these oscillations are very obvious and are seen immediately even by naive observers, under other conditions they are very subtle. They involve an aspect of the stimulus to which one does not normally attend and the more subtle oscillations, notably the higher intensity two-population oscillations and the cone oscillations, often involve one or two practice

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sessions before they are noticed. The learning which occurs presumably involves primarily a redirection of attention.*

MATCHING CRITERIA

It was found that a perfect match between the test and matching fields was not possible. The perception produced by a train of real-light pulses can be analyzed into at least two separate perceptions. On the one hand there is what might be called the "sense of light modulation." This is simply the rather analytical perception that the light intensity level is increasing and decreasing over time. On the other hand, there is what might be called the "sense of pulsation" which is the "throbbing" aspect of pulsed light. With real-light pulses, there is a certain relationship or ratio between the magnitudes of these two sensations. The auto-oscillations produced by a single pulse can also be divided into a "sense of light modulation" and a "sense of pulsation." However, in this case, the relationship between the two is somewhat different. Except for the purely cone-generated oscillations, the "sense of pulsation" seems to be inordinately large with respect to the "sense of light modulation." Inordinately large, that is, when compared to the relationship that exists between these two sensations for a train of real-light pulses.** Accordingly, data were collected under two different criteria. Under Criterion I, the observers attempted to match the sense of pulsation in the test field by adjusting the amplitudes of the matching pulses. Under this criterion, the inter-pulse intervals

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* It's difficult to describe, behaviorally, just what changes occur during the learning which allows one to see some of these more subtle oscillations. However, it seems to be important to avoid the oculomotor "alerting" responses which normally occur in response to pulsed stimuli. In order to avoid this diversion of attention, one tries to adopt a sort of "distant stare" which perhaps results in the temporary suspension of microsaccades and (in the case of peripheral stimuli) the suspension of the incipient macrosaccade which normally occurs in response to a pulsed stimulus.

** The auto-oscillations are really oscillations of the iconic after-image and the difference in quality between this iconic after-image and the sensation produced by a real-light stimulus may underlie the altered relationship between the "sense of pulsation" and the "sense of light modulation." Another difference between the auto-oscillations and the matching pulses was that, with all of the strongest auto-oscillations, their downward swings were stronger than could be produced by the matching pulses.

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were always set at .5 seconds. This was done for two reasons. First, the strength of the "sense of pulsation" produced by real-light pulses is determined not only by the amplitudes of the pulses but also by the temporal spacing between them. Holding the inter-pulse interval constant at .5 seconds allowed a uni-dimensional, and therefore more straightforward, comparison of the data from the different conditions. Secondly, in some cases, it was impossible to match both the amplitudes and the inter-flash intervals of the auto-oscillations produced by the test flashes. That is, in some of the two-population cases where the sense of pulsation in the test field was exceptionally strong, no amount of real-light modulation in the matching field was able to match the sense of pulsation produced in the test field unless the frequency of the pulses in the matching field was reduced below the perceived frequency of the test field oscillations; in addition to 100% modulation, the matching field pulses had to be further separated in time in order to make them more distinct. Under Criterion II, the observers attempted to match the "sense of light modulation" and the perceived inter-flash intervals of the auto-oscillations.

Although the auto-oscillations could not be matched for both the "sense of light modulation" and the "sense of pulsation" at the same time, the first peaks of the test field could be quite well matched in terms of both criteria at the same time. Consequently, as the data will show, the first peaks of the matching waveforms are quite similar under both criteria for a given set of test field conditions.

ADAPTATION

In the fully dark adapted state, auto-oscillations are weak or non-existent. Figure 2 (page 16) shows the matching stimulus to a 4 photopic troland, 460 nm, $1\frac{1}{2}^0$ test pulse located 2^0 from the fovea with the observer fully dark adapted. Matches were made using Criterion II.

The strongest auto-oscillations, on the other hand, occur at moderate adaptation levels, i.e., with rhodopsin bleaches of between approximately 5 and 25%. For example, Figure 3 (page 17) shows the Criterion I matches for subject FH to a 4 photopic troland, 460 nm, $1\frac{1}{2}^0$ test pulse located 2^0 from the fovea. In 3(a), the adaptational state was a 7% bleach produced by 5 minutes of adaptation to a 3,700 scotopic troland field followed by 1 minute of dark adaptation. In 3(b), the test pulse is the same and the rhodopsin bleaching level is also 7%. However, this 7% bleach was produced by 11 minutes of exposure to 14,000 scotopic trolands followed by 11 minutes of dark adaptation. A comparison of (a) and (b) shows the effect of the recency of the bleach since in all other respects the conditions were the same. It can be seen that the more recent bleach produces the stronger auto-oscillation. The data for

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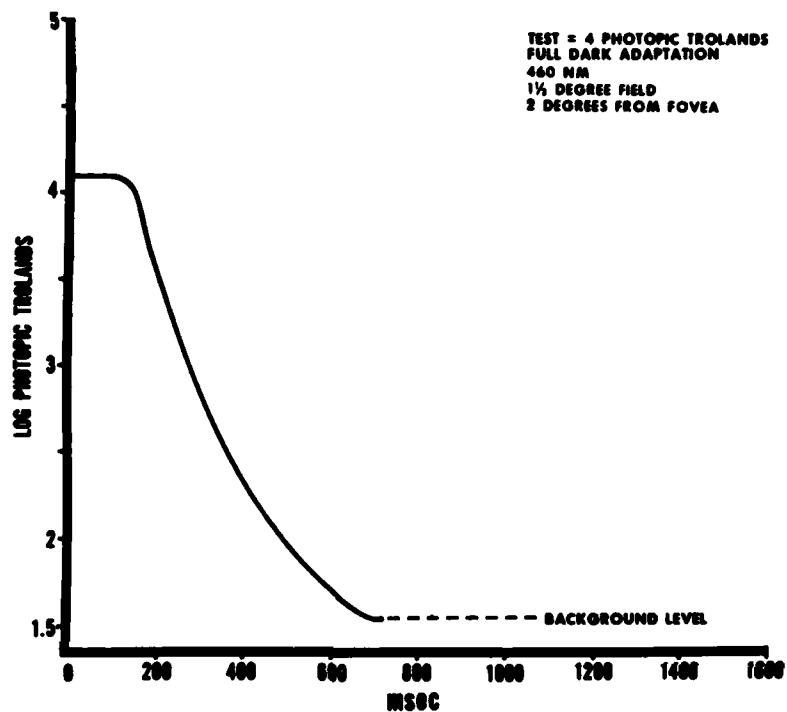
FIGURE 2. The matching stimulus for subject FH to a 4 photopic troland, 460 nm, $1\frac{1}{2}^0$ test stimulus presented 2^0 from the fovea with the observer fully dark adapted.

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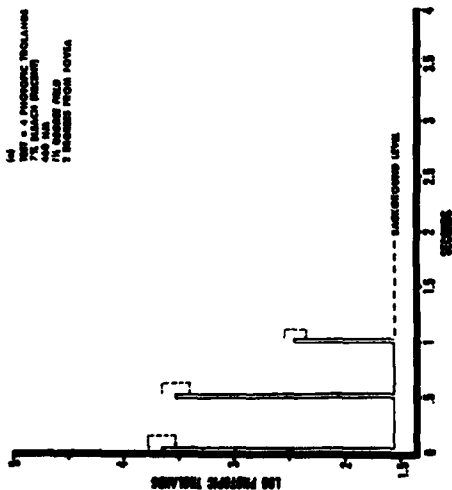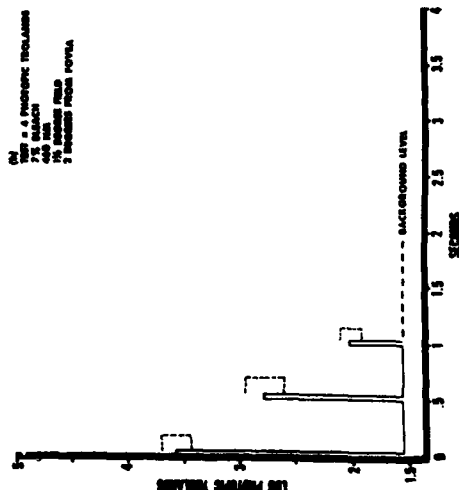
FIGURE 3. In (a), test pulse conditions are as shown. A 7% bleaching level was produced by 5 minutes of adaptation to 3,700 scotopic trolands followed by 1 minute of dark adaptation. In (b), test pulse conditions are the same and the bleaching level is again 7%, but was produced by 11 minutes of exposure to 14,000 scotopic trolands followed by 11 minutes of dark adaptation. The more recent bleach produces the stronger auto-oscillation. Data is from observer FH using Criterion I. The matching pulses shown are the average of four trials and the error in these judgments is indicated by the dashed lines. The first matching pulses are of much greater intensity than the test pulses because of the higher state of light adaptation in the matching eye and the background used with the matching field.

subject VR are similar and are shown in Figure 4 (page 19). The patterns in Figure 5 (page 20) are the Criterion II matches (subject FH) for the same stimulus and adaptational conditions. The two types of 7% bleach produced similar patterns with respect to this criterion. For subject FH, the patterns shown in Figures 3 (page 17) and 5 (page 20) were the best matches on about 50% of the trials. On approximately 40% of the trials, only two pulses in the matching stimulus constituted a better match and on approximately 10% of the trials 4 pulses constituted a better match. The corresponding percentages for subject VR were about 65, 30 and 5%. Of course, the cone pigments have a time constant of regeneration (t_0 = approximately 70 seconds, Rushton, 1964) which is different from that of rhodopsin so that although the rhodopsin bleach levels were held constant in the two different bleaching conditions the cone pigment bleaching levels were not. This, however, does not seem to be what produces the response difference between the two different conditions since, as described later, the recent 7% bleach produces a stronger auto-oscillation even when rods alone are responding.

Over a limited range, it was found that when threshold is increased, a proportional increase in stimulus intensity produces a similar (albeit a little stronger) oscillation pattern. For example, an adaptation regimen which produced a fivefold increase in threshold over that produced by 10 minutes of adaptation to 14,000 scotopic trolands followed by 10 minutes of dark adaptation resulted in a similar oscillatory pattern when the intensity of the test flash was raised by a factor of five. However, when the threshold was increased by a factor of twenty over that produced by the former adaptation regimen, no intensity could be found which produced a similar oscillatory pattern.

BACKGROUND TO OTHER EYE

Figure 6 (page 21) (Criterion I) shows that these oscillations are unaffected by a background presented to the other eye. In this case, conditions were the same as in Figure 3(a) (page 17) except that a white, steady, 20 photopic troland background was presented to the right eye for five seconds during which time the test pulse was presented to the left eye. The matching data for subject FH shows little difference from that shown in Figure 3(a) (page 17). The results for subject VR are shown in Figure 7 (page 21).

INTENSITY

For each of the different adaptational states and test pulse chromaticities, there is an intensity which produces the maximum amplitude auto-oscillation. With mixed-population and rod-only responses, as intensity is raised beyond this point the auto-oscillations tend to become

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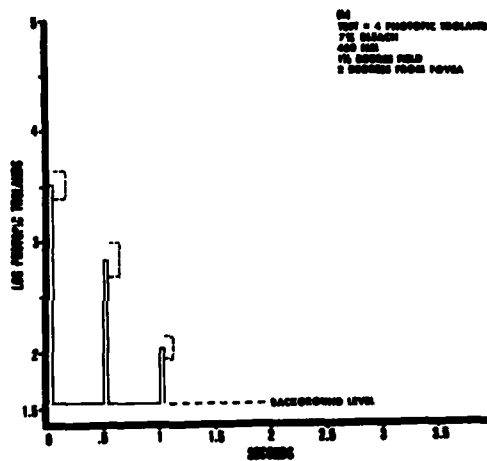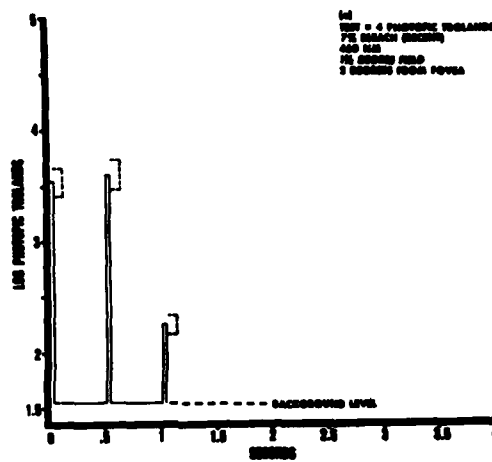
FIGURE 4. Data from subject YR. Conditions are the same
as in Figure 3 with (a) being the more recent bleach.

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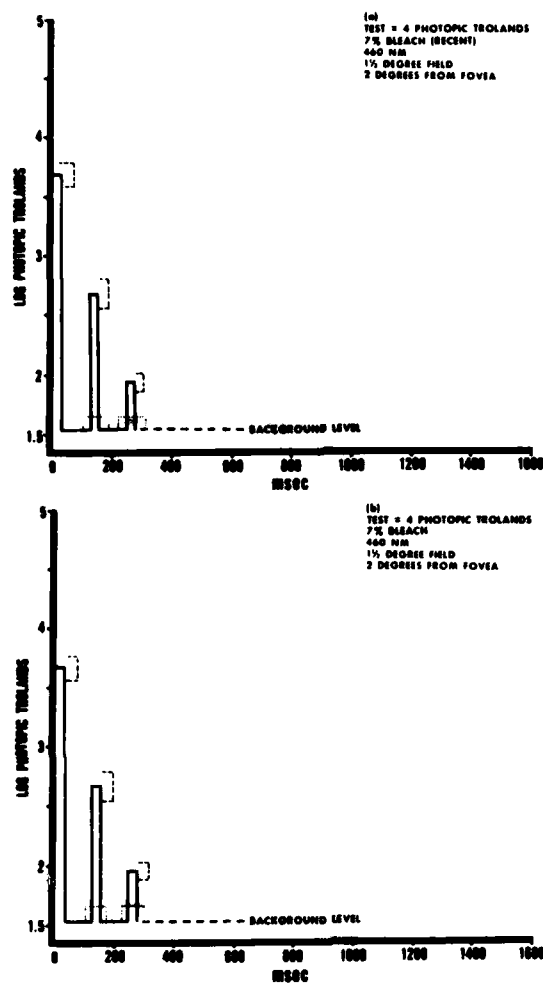
FIGURE 5. Criterion II matches for observer FH. Condi-
tions are the same as in Figure 3 with (a) being the more
recent bleach. The two types of 7% bleach produce similar
patterns with respect to this criterion. The dashed lines
indicate the amplitude variability and the dotted lines
indicate the temporal variability of the pulses.

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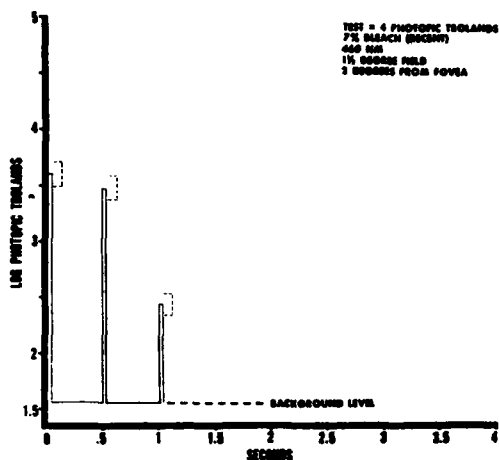
FIGURE 6. Conditions
were the same as in Figure
3(a), except that the
right eye was presented
with a 20 photopic tro-
land, white background.
The matching pattern shows
little difference from
that in Figure 3(a). Ob-
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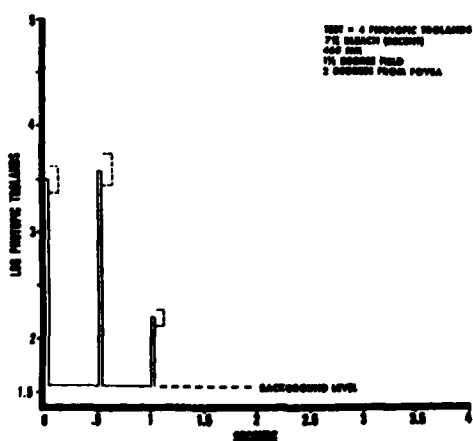
FIGURE 7. Data from sub-
ject VR. Conditions are
the same as described in
Figure 6.

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smaller in amplitude but greater in number. For example, Figure 8(a) (page 23) shows a typical Criterion I match to a 460 nm, 1½° pulse of 12 photopic trolands presented 5° from the fovea with the eye at a 7% recent bleach. There are five pulses here with the variability being such that anywhere from four to six pulses were obtained on a given trial. Figure 8(b) (page 23) shows a typical Criterion I match where the conditions are the same except that the intensity has been raised from 12 photopic trolands to 34. Here there are seven pulses with the range being anywhere from six to eight pulses. Figures 9(a) and 9(b) (page 24) are the corresponding Criterion II matches. At the higher intensity the first peak "hangs-up" somewhat, i.e., there is a delay before the subsequent oscillations begin and this is reflected in the extended duration of the first matching pulse.

A more complete analysis of the relationship between intensity (scotopic trolands) and auto-oscillation strength is shown in Figure 10 (page 25). Auto-oscillation strength was determined by obtaining, at various stimulus intensities, matching data according to Criterion I and then summing the intensities of the second and third pulses of each match. The highest peaks were achieved at 180 scotopic trolands for the 460 nm stimulus, 155 scotopic trolands for the 555 nm stimulus, and 65 scotopic trolands for the 620 nm stimulus.

For the 620 nm stimulus, as intensity is raised above threshold there is an interval in which only the cones respond and the greatest amplitude of the cone-only oscillations occurs at about .06 scotopic trolands. As intensity is increased further, one begins to see a rod response which at first dampens the oscillations producing a dip in the neighborhood of .15 scotopic trolands. Eventually, the rod response enhances the oscillations and another peak is produced at about 65 scotopic trolands. The pattern for the 460 nm stimulus is similar except that the peak at the left is a rod-only response which is dampened by the incipient cone response and then rises to peak at about 180 scotopic (6.6 photopic) trolands. The 555 nm stimulus produces strong rod and cone contributions from the beginning and instead of showing a dip, remains constant for awhile and then rises to peak at about 155 scotopic trolands. It is quite clear that the intensities at which the two-population oscillations peak are primarily rod-determined since they peak relatively close to each other in terms of scotopic retinal illuminance in spite of their vastly different photopic values at these peaks (the 620 nm stimulus, for example, peaked at a photopic retinal illuminance that was some 180 times greater than that of the 460 nm stimulus at its peak). It is just as clear, however, that the peak amplitudes achieved by the two-population oscillations are not solely rod-determined since the peaks for the different chromaticities are not all at the same height. The very large cone response produced by the 620 nm stimulus apparently reduces the amplitude of these auto-oscillations.

22
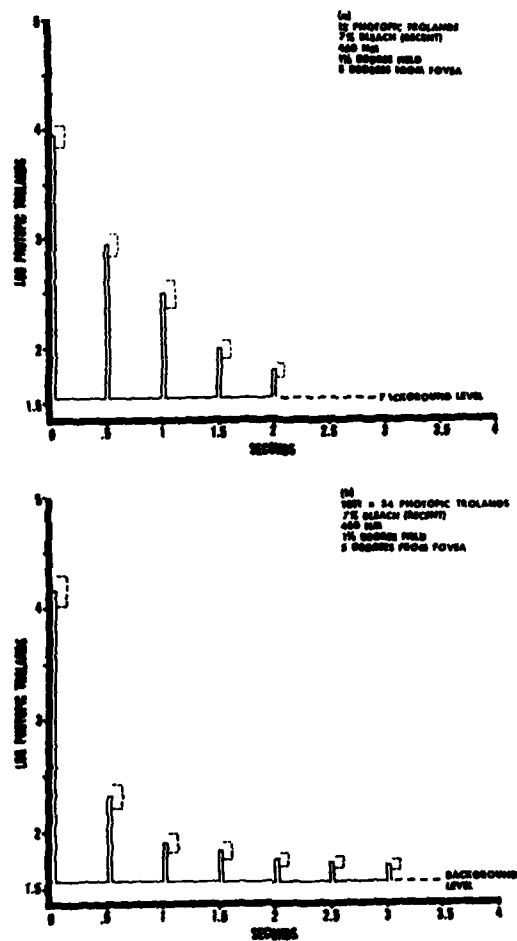
FIGURE 8. (a) is the Criterion I match to a 12 photopic troland stimulus and (b) is the Criterion I match to a 34 photopic troland stimulus for subject FH. The other conditions (as shown) are the same for both. As intensity is increased, the oscillations become smaller in amplitude but greater in number.

23
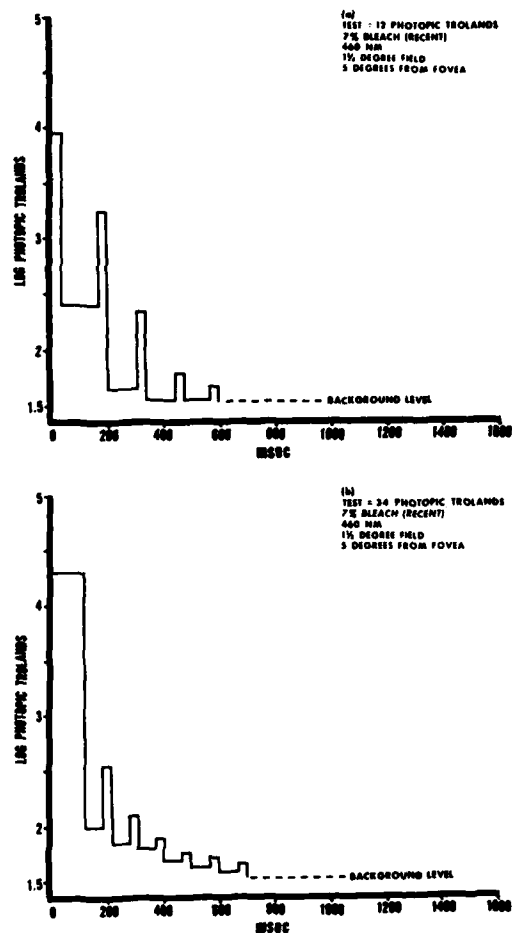
FIGURE 9. The Criterion II matches for the conditions described in Figure 8 (subject FH). (a) is the match to the 12 photopic troland stimulus and (b) is the match to the 34 photopic troland stimulus.
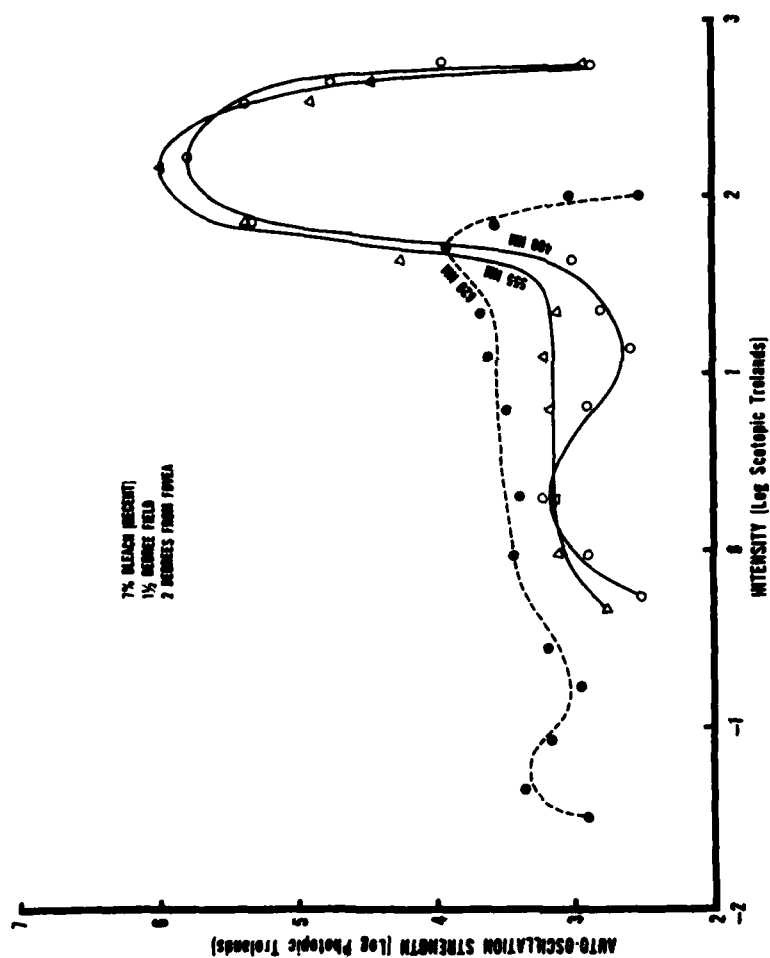
FIGURE 10. Auto-oscillation amplitude as a function of scotopic retinal illuminance for three different chromaticities and a recent 7% rhodopsin bleach (observer FH). Data were generated by summing the second and third pulses of the matching stimuli.

25

RETINAL LOCUS

As one moves from a central to a more peripheral retinal locus, rod density increases (up to about 15^0) and there is a corresponding increase in brightness for equiluminance targets under, for instance, the chromaticity and adaptation conditions of Figures 3 (page 17) through 9 (page 24). Does such a change in retinal locus have the same effect as a change in test pulse intensity, insofar as these oscillations are concerned? The answer seems to be: almost. Figure 11 (page 27) shows the Criterion I matches to the same 460 nm, 4 photopic troland, $1\frac{1}{2}^0$ target presented at 2 and 8^0 eccentricity with the eye at a 7% recent bleach. Moving to the 8^0 locus produces more but shallower oscillations just as does holding the retinal locus constant and raising the intensity (Figure 8, page 23). The corresponding Criterion II matches are shown in Figure 12 (page 28). In Figure 13 (page 29) the same targets are presented at the 2 and 8^0 loci except that the intensity at the 8^0 locus has been reduced to 1.3 photopic trolands so that the brightness at this locus matches that at the 2^0 locus. It can be seen that the two patterns are similar but the auto-oscillations at the 8^0 locus are somewhat weaker than at the 2^0 locus. Of course, the cone response is weaker at the 8^0 locus than at the 2^0 locus and the fact that this weaker cone response is associated with weaker oscillations indicates that although the cone response is manifest only in the first peak (as indicated by the phenomenology)* it actually affects the magnitude of later peaks. The Criterion II matches are shown in Figure 14 (page 30). On the other hand, raising the intensity of the 8^0 locus to 12 photopic trolands produced a pattern similar to that of Figure 9(b) (page 24).

SINGLE-POPULATION OSCILLATIONS

Criterion I matches to purely rod-generated auto-oscillations, in which the stimulus was below cone threshold, are shown in Figure 15 (Page 31). The stimulus in both cases was a .1 photopic (2.4 scotopic) troland, 460 nm, $1\frac{1}{2}^0$ target presented 5^0 from the fovea. The only difference is that the adaptational state for 15(a) was a recent 7% bleach and that for 15(b) was an old 7% bleach. It is seen that the former produced stronger auto-oscillation than did the latter. Figure 16 (page 32) shows the Criterion II matches to these rod generated auto-oscillations.

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* When both populations are responding, one soon notices that there is an initial chromatic portion from the shorter-latency cones followed by an achromatic portion from the rods. The phenomenology of the response provides several clues and will be discussed in more detail in the next section.
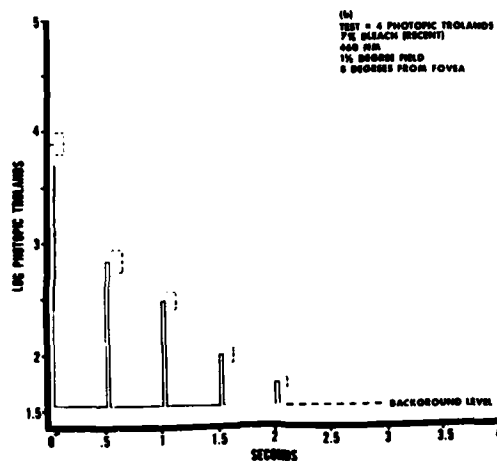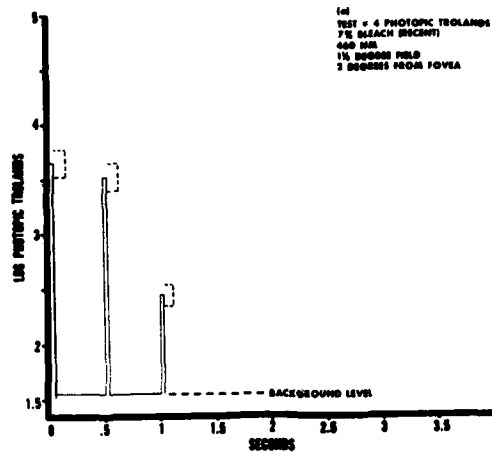
FIGURE 11. In (a) the target is presented at a 2^0 locus
and in (b) it is presented at an 8^0 locus (observer FH).
Other conditions are the same (as shown). It is seen
that moving to a more peripheral locus, which produces
a brighter response, has a similar effect to increasing
the intensity at the more central locus (Figure 8).

27
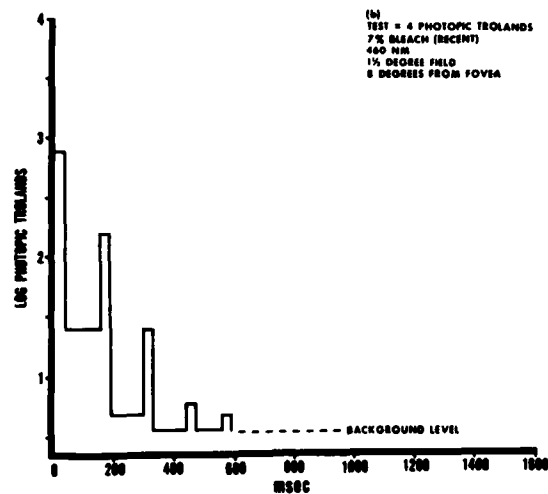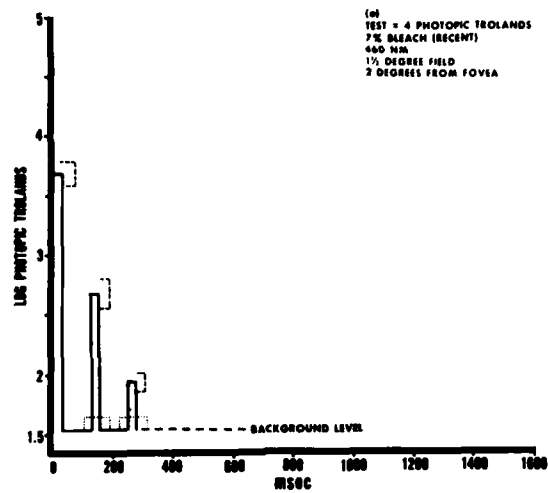
FIGURE 12. The Criterion II matches to the conditions
described in Figure 11 (observer FH). (a) is the match
to the 2^0 locus and (b) is the match to the 8^0 locus.

28
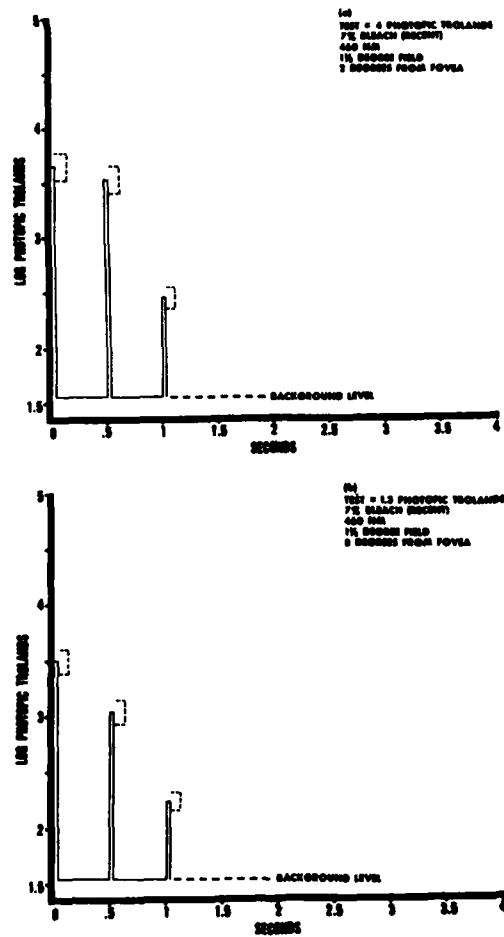
FIGURE 13. Conditions are the same as in Figure 11 except
that the intensity of the more peripheral target (b) has
been reduced so that its brightness appears equal to that
of the more central target (a). The auto-oscillations are
similar, but slightly weaker, at the more peripheral locus.

29
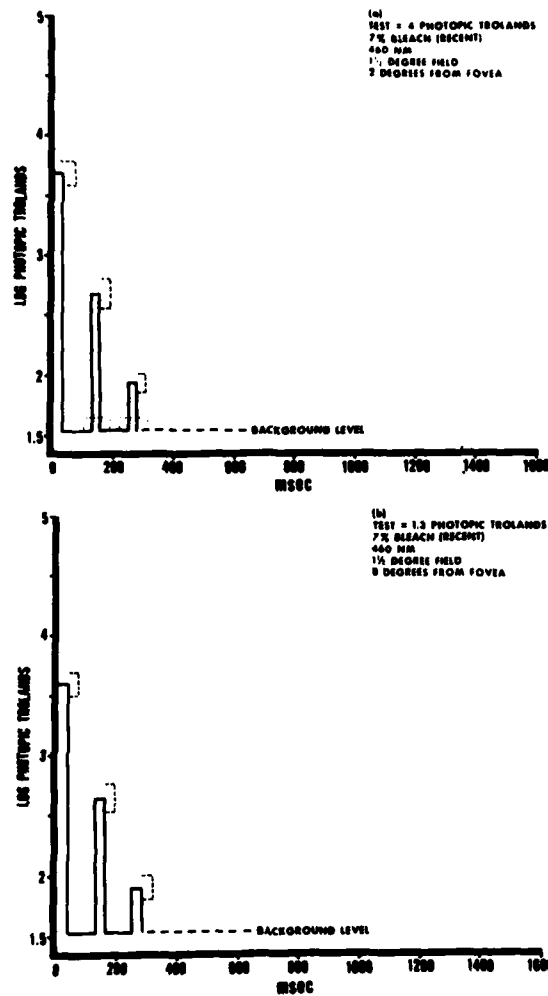
FIGURE 14. The Criterion II matches to the conditions
described in Figure 13 (observer FH).

30
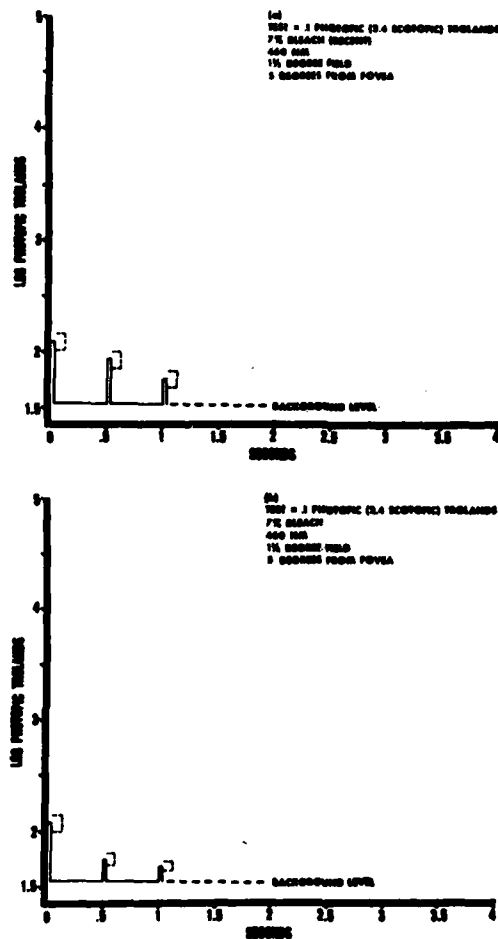
FIGURE 15. Criterion I matches to purely rod-generated auto-oscillations produced by a .1 photopic troland, 460 nm, $1\frac{1}{2}^0$ target presented 5^0 from the fovea. The auto-oscillations produced by the recent 7% bleach (a) are stronger than those produced by the old 7% bleach (b).

31
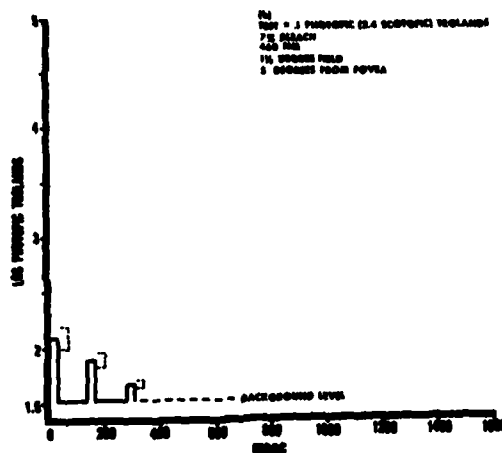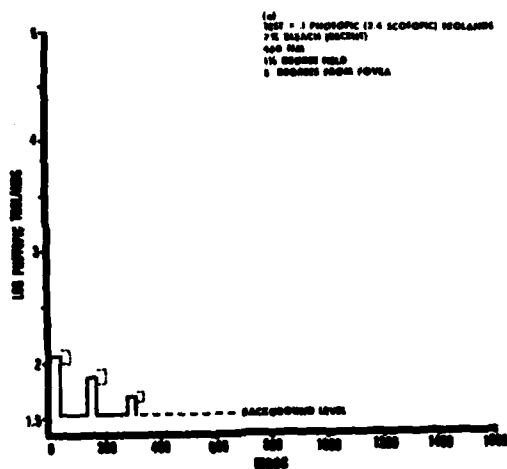
FIGURE 16. The Criterion II matches to the rod-generated auto-oscillations described in Figure 15.

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Figure 17(a) (page 34) (subject FH) shows the Criterion I match to purely cone-generated* oscillations produced by a 680 nm, 20 photopic troland, $\frac{1}{2}^0$ stimulus centrally viewed with the eye at a 33% rhodopsin bleach. The $\frac{1}{2}^0$ size was selected in order to encompass a completely rod-free (Heath, 1958) area of the retina. The conditions are the same in 17(b) except that here Criterion II was used.

It is seen that, for the cone-generated auto-oscillations, Criterion II (sense of light modulation) requires more modulation in the matching stimulus than does Criterion I. That is, for the cone oscillations, the sense of light modulation is of greater magnitude than the sense of pulsation, whereas just the opposite is true for the strongest mixed-population oscillations.

DELAYED OSCILLATIONS

Under certain conditions where both rods and cones are active, one sometimes sees a curious long-delayed oscillation. For example, with a 2% bleach produced by 11 minutes of light adaptation followed by 20 minutes of dark adaptation, a 620 nm, 1 photopic troland, $1\frac{1}{2}^0$ test field presented 2^0 from the fovea yielded, on about 15% of the trials, the pattern (Criterion II) shown in Figure 18 (page 35): the initial flash followed about .6 seconds later by a second (albeit very weak) oscillation. In the other approximately 85% of the trials, there was no second peak.

Under a different set of conditions, one occasionally (on about 5% of the trials) sees a rather elaborate version of this delayed-flash pattern as shown in Figure 19 (page 35) (Criterion II). There is an initial flash followed by some small perturbations and then a second large flash followed by another small perturbation. This was produced by a 200 photopic troland, 460 nm, $1\frac{1}{2}^0$ field presented 6^0 from the fovea immediately after a 23% rhodopsin bleach in which the adapting source (tungsten) was changed to a daylight color temperature by means of a daylight correcting filter. Here, the first flash is chromatic and the second major flash and the small perturbations in between appear achromatic. Presumably, the conditions described in Figure 18 (page 35) also produce small perturbations between the two peaks but they are below threshold. It is probably more than coincidental that both instances of a delayed achromatic response are associated with an increased cone response relative to the rod response (when compared to the other two-population auto-oscillations described previously) achieved by using either a longer wavelength stimulus (Figure 18) or a higher state of light adaptation (Figure 19, page 35).

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* The existence of purely cone-generated oscillations was reported by the author at ARVO in 1978 and has also been reported by Bowen, R.W., Markell, K.A. and Schoon, C.M., J. Opt. Soc. Amer., 70(12), 1453-1458, 1980.
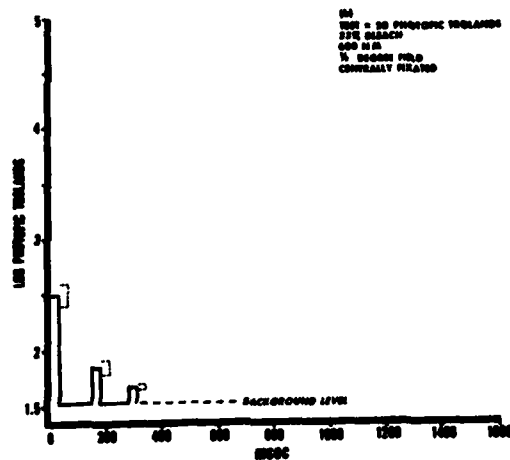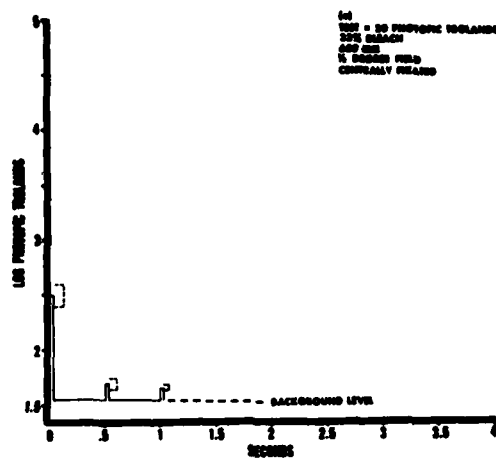
FIGURE 17.   The match, for subject FH, to cone-generated
oscillations produced by a 680 nm, 20 photopic troland,
½⁰ stimulus centrally viewed with the eye at a 33% rhodopsin
bleach.   Criterion I was used for (a) and Criterion II for
(b).

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TEST = 1 PHOTOPIC TROLAND
2% BLEACH
620 NM
1¼ DEGREE FIELD
2 DEGREES FROM FOVEA
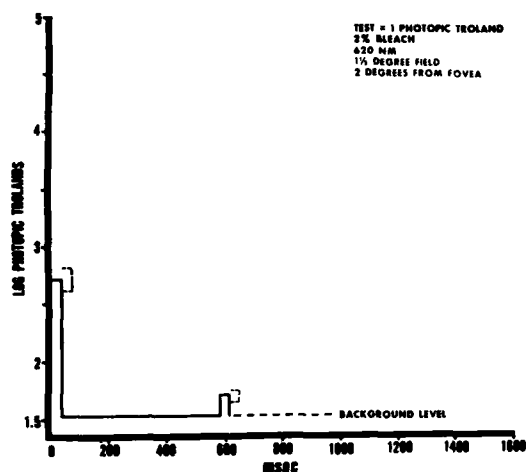
FIGURE 18. A Criterion
II match for subject FH
to a 620 nm, 1 photopic
troland $1\frac{1}{2}^0$ test field
presented 2^0 from the
fovea with the eye at a
2% bleach. There is a
long (approx. .6 sec)
delay before the auto-
oscillation. The first
flash is chromatic and
the second flash is nearly
achromatic.

TEST = 200 PHOTOPIC TROLANDS
23% BLEACH
460 NM
1¼ DEGREE FIELD
6 DEGREES FROM FOVEA
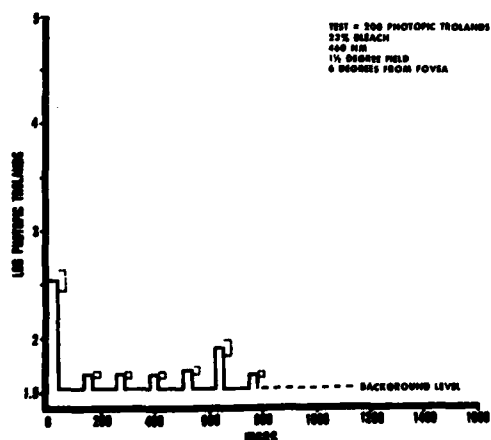
FIGURE 19. The Criterion
II match to a complex
auto-oscillation produced
by a 200 photopic troland,
460 nm, $1\frac{1}{2}^0$ target pre-
sented 6^0 from the fovea
immediately after a 23%
rhodopsin bleach by a day-
light corrected source.

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ROD-CONE SILENT SUBSTITUTION

One stimulus-adaptation combination which does not produce auto-oscillation was described earlier (Figure 2, page 16). The Criterion II match to another such combination is shown in Figure 20 (page 37). A 20 photopic troland, 680 nm, $1\frac{1}{2}^0$ test pulse was presented 8^0 from the fovea with the eye at a 2% bleach. Here, the rods and cones are responding approximately equally and the rod response simply blends into the cone response constituting, in effect, a silent substitution for it. That is, one first sees the chromatic cone response and then the achromatic rod response and no oscillation.

The overall shape of the response was determined in the usual way with the complex waveform synthesizer. In order to obtain an estimate of how the total response is apportioned between the rod and cone responses, one of the left eye channels was used to present a 690 nm real-light stimulus followed immediately by a white real-light stimulus from the other left eye channel. After strong light adaptation, the observers adjusted the duration of each to match the perceived division between the cone (chromatic) and rod (achromatic) responses produced by the single 680 nm test pulse. The wide line represents the approximate cone portion and the narrow line the approximate rod portion.

EXTENDED DURATION PULSES

Figure 21 (page 37) shows the Criterion II match to a 460 nm, $1\frac{1}{2}^0$, 174 photopic troland stimulus of extended duration (.4 seconds). The stimulus was presented 5^0 from the fovea and the observer was fully dark adapted. There is a half-cycle oscillation at the onset of the stimulus and several at its offset. Although full dark adaptation produces little or no auto-oscillatory activity, a stimulus which is of sufficient intensity and/or duration to produce significant adaptation can result in low level oscillatory activity at its offset. Similar oscillations at stimulus offset were produced by a 400 msec, 4 photopic troland, $1\frac{1}{2}^0$, 460 nm field presented 8^0 from the fovea under conditions of a 7% recent bleach (Figure 22, page 38).

MATCHING EXPERIMENTS (EQUIVALENT BACKGROUND)

Equivalent backgrounds are not equivalent insofar as these oscillations are concerned. An attempt was made to reproduce the strong two-population oscillations described in Figure 3(a) (page 17) by using the same viewing and stimulus conditions and a background, with the subject fully dark adapted, equivalent to this 7% recent bleach. Test pulses were presented 2 seconds after the background light was turned on and 60 seconds after the background light was turned on and the observers

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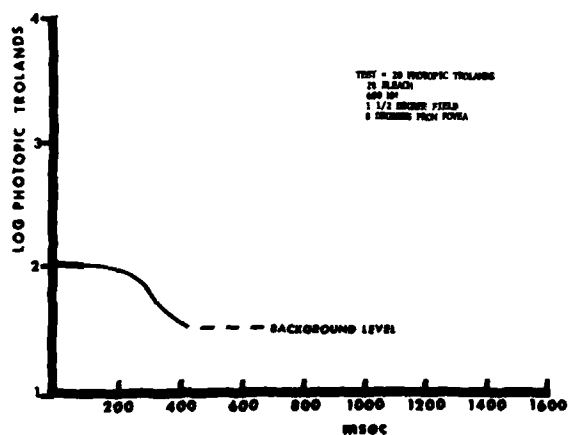
FIGURE 20. The match for subject FH to a test pulse under the conditions shown. The wide line represents approximately the cone portion and the narrow line represents approximately the rod portion.
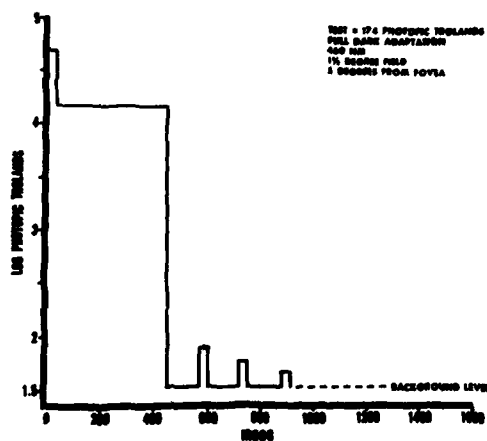
FIGURE 21. The Criterion II matching pattern for subject FH to a pulse of extended duration (.4 sec.) presented under conditions of full dark adaptation.

37
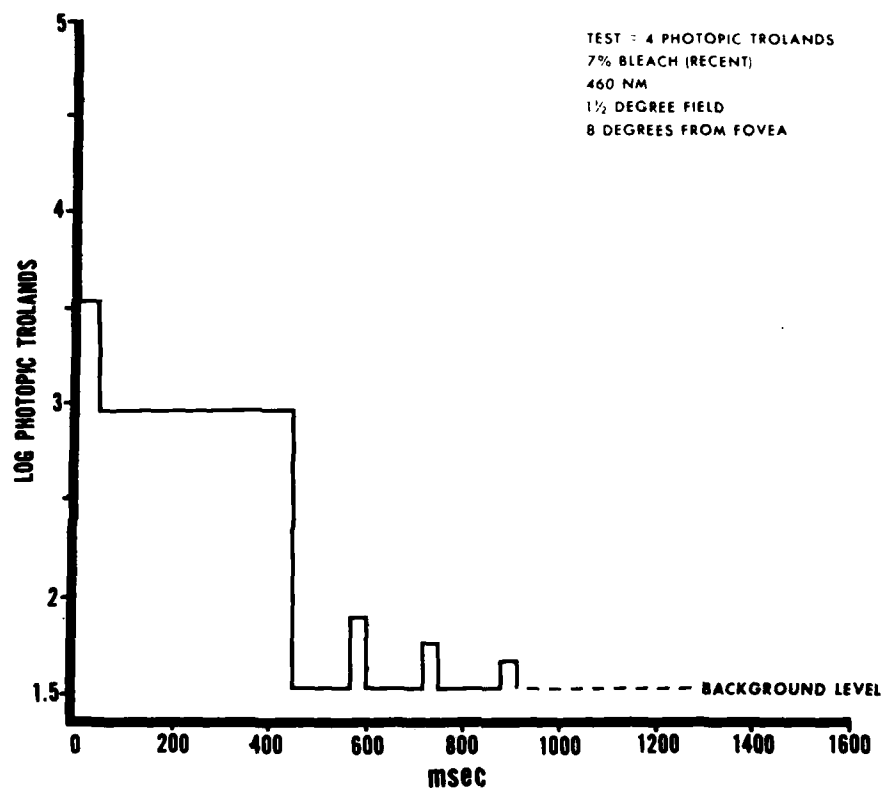
FIGURE 22. The Criterion II matching pattern for subject FH to a pulse of extended duration (.4 sec.) presented under mesopic adaptational conditions.

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TEST = 4 PHOTOPIC TROLANDS
BACKGROUND = 8 PHOTOPIC TROLANDS (WHITE)
460 NM
1½ DEGREE FIELD
2 DEGREES FROM FOVEA
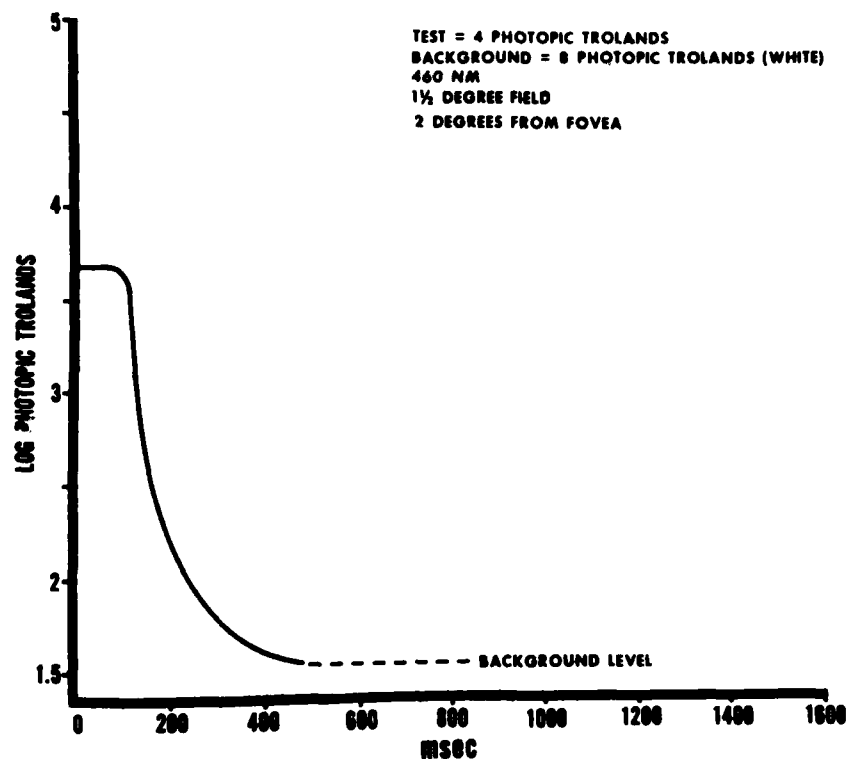
FIGURE 23. The matching stimulus to a 460 nm, 4 photopic troland, $1\frac{1}{2}^0$ test pulse presented 2^0 from the fovea with a background equivalent to a 7% recent bleach. On most trials, no oscillations were seen when the test pulse was presented either 2 seconds after the background was turned on or 60 seconds after the background was turned on.
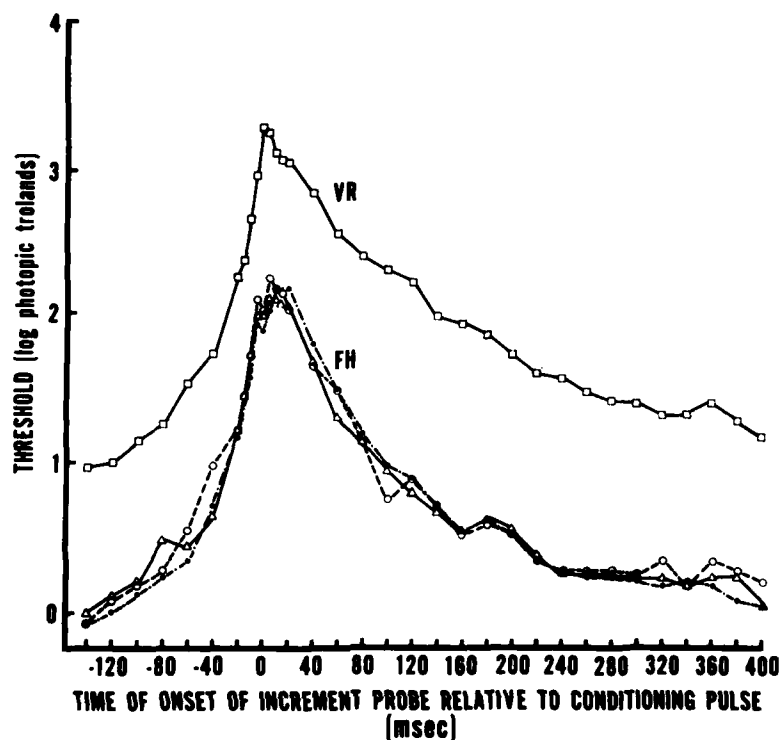
FIGURE 24. The threshold of a 560 nm, $\frac{1}{2}^0$, 10 msec increment probe centered on and presented before, during, and after a conditioning pulse which produced strong auto-oscillation (555 nm, $1\frac{1}{2}^0$ pulse presented 3^0 from the fovea with the eye adapted to a 7% recent bleach). The three individual trials are shown for observer FH. The curve for VR is the average of three trials and is raised one log unit. Observers used the method of adjustment with ascending trials only.

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made matches using Criterion II. On most trials, no oscillations were seen under either condition (Figure 23, page 39). On about 25% of the trials, one very weak auto-oscillation was seen.

INCREMENT THRESHOLD EXPERIMENTS

The three individual increment threshold trials for subject FH are shown in Figure 24 (page 40). There would seem to be a significant secondary peak at approximately 180 msec and possibly another one around 360 msec. Only an average of the three trials for subject VR is shown since his data indicated no reliable secondary peaks except possibly one at 360 msec. Although only FH showed an elevation at 180 msec, both subjects indicated difficulty in making the judgment at this point requiring about two or three times as long to make the setting at this time as at the others. Regardless of whether or not there are any significant secondary peaks, the important point would seem to be that they are very weak when compared to the other psychophysical data which, under similar conditions, indicates secondary peaks approximately as strong as the primary ones.

DISCUSSION

The strength of the auto-oscillations depends upon: 1) the adaptational state of the eye, 2) the degree to which both rods and cones are participating, 3) the intensity of the stimulus and, 4) the duration of the stimulus. With increasing light adaptation, the oscillations first increase in amplitude and number and then decrease. The importance of adaptational state is probably closely related to its effect upon temporal resolution. It is well known that temporal resolution increases with increasing light adaptation (Lythgoe and Tansley, 1929). This is true not only for the system as a whole but also within each photoreceptor population as Brindley (1960) has shown for cones and as Conner and MacLeod (1977) have shown for rods. It would seem that in the process of acquiring this shorter time constant the system becomes* more "bouncy" (less damped), just as is the case in some physical systems.* Of course, a

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* In a similar vein, Alpern (1968) has likened light adaptation to the tightening of the suspension in a galvanometer. When the suspension is tightened, temporal resolution increases and sensitivity decreases and as the suspension is loosened sensitivity increases at the cost of temporal resolving power. It might also be added that a tightening of the suspension could increase the ringing or "bounciness."

high degree of light adaptation also has the effect of virtually elimi-
nating rod participation which, in turn, has the effect of reducing the
magnitude of the oscillations. Thus, the moderate adaptational levels
which produce the strongest auto-oscillations for peripheral stimuli
would seem to represent a compromise between these two effects.

It would seem almost certain that these oscillations are retinally
generated. It is difficult to imagine that adaptation, surely a retinal
process (in the simple sense of sensitivity to photic flux), would be
such a crucial variable to the oscillations if they were not generated
in the retina or that the form of the oscillations would depend to such
a great extent upon the relative participation of rods vs cones. Also,
the fact that a background presented to the same eye greatly reduces or
eliminates the oscillations but a background presented to the other eye
has no effect on them is consistent with a retinal-origin hypothesis.
However, the increment threshold data indicates that these oscillations
do not originate in the receptors. It is thought that increment thresh-
olds are determined very early in the visual system, probably in the re-
ceptors themselves (Boynton, 1972). The very minimal effect of the auto-
oscillations upon the increment threshold is evidence that the auto-oscil-
lations are generated at a more proximal stage than this. A non-receptor
origin of these oscillations is also indicated by the finding (Figure 13,
page 29) that when the stimulus is moved from the 2^0 locus to the 8^0
locus, a similar oscillatory pattern is produced at the 8^0 locus only
if the stimulus illuminance is reduced to the point where its brightness
is equal to that at the 2^0 locus. If these oscillations were generated
in the receptors, one would expect that similar oscillatory patterns
would be produced by holding constant the illuminance, i.e., the amount
of light flux impinging upon the receptors. Instead, similar oscilla-
tory patterns are produced by holding constant the activity at some
brightness-determining pooling site.

If these oscillations do result from a "ringing" in a transient
network, then the inner plexiform layer would seem to be implicated be-
cause of its known role in the processing and enhancement of stimulus
transients or temporal information. Dowling (1967) has made a distinc-
tion between bleaching adaptation (long-term) and neural adaptation
(short-term). Although long-term adaptation also produces changes in
neural organization (Barlow, Fitzhugh, and Kuffler, 1957), presumably a
more recent bleach involves a strictly neural component. The importance
of this additional neural component to transient processing is indicated
by the fact that a recent bleach produces stronger auto-oscillations
than an old bleach when the level of bleach at the time of measurement
is held constant. Dowling (1967) has also described an amacrine-bipolar
feedback loop which he believed to be involved in adaptation. When we
consider: 1) the relationship of adaptation to these oscillations, 2)
the involvement of the amacrine-bipolar feedback loop with the inner
plexiform layer and, 3) the potential oscillatory nature of negative

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feedback systems, an interesting possibility is suggested, i.e., that these oscillations originate in this amacrine-bipolar feedback loop.

As it turns out, Wachmeister and Dowling (1978) in work with the mudpuppy, have recently reported evidence indicating that oscillatory potentials may originate in two different feedback systems: 1) the amacrine-bipolar, amacrine-perikayra, or amacrine-amacrine system, and 2) the feedback system created by the recently discovered interplexiform cell, which is presynaptic to amacrine cell processes in the inner plexi-form layer and to bipolar cell dendrites and horizontal cell processes in the outer plexiform layer. Their evidence is based upon the various depths at which the oscillatory potentials can be recorded and their pat-tern of polarity reversals which, they point out, seem to reflect radial flows of current within the retina. Some transretinal ERG oscillatory potentials which they recorded are shown in Figure 25 (page 44). Oscil-latory potentials have also been recorded in the human ERG (e.g., Cobb and Morton, 1953 and Genest, 1964) and these studies, as well as the mudpuppy work of Wachmeister and Dowling, are in agreement with the pre-sent psychophysical oscillatory data in reporting that: 1) up to seven oscillations can be reliably produced and 2) these oscillations are strongest under mesopic adaptational conditions.

It is important to note, however, that the oscillatory potentials recorded in the human ERG (Figure 26, page 44) are approximately an order of magnitude higher in frequency than those reported in the present psy-chophysical work. (A comparison of Figures 25, page 44, and 26, page 44, reveals, however, that the ERG OPs of the mudpuppy are much slower than those of the human.) Furthermore, if oscillations recorded in the optic tract of the monkey (Doty and Kimura, 1963) (Figure 27, page 45) can be generalized to human, they also have a high frequency at this stage. However, occipital e.e.g. recordings in the human (Cobb and Dawson, 1960; Walter, 1961) have shown oscillatory potentials of approximately 10 Hz. It is suggested, then, that the oscillations arriving at the cortex are momentarily stored and then "read-out" at the slower natural frequency of the occipital cortex.

This idea of a "slowing down" is supported by several investigations which have found that, at high frequencies, the perceived rate of a flick-ering photic stimulus is much lower than the actual rate. For example, Le Grand (1937) reported that a stimulus flickering in the periphery at an actual rate of 42 Hz appeared to be flickering at a rate of only 7 Hz. Also, Fukuda (1977) presented flickering photic stimuli and asked observ-ers to adjust the frequency of an audio flutter stimulus until its fre-quency appeared to match that of the photic flicker. He found that observers never set the frequency of the matching stimulus above 10 Hz even though the frequency of the photic flicker went as high as approxi-mately 50 Hz. Since the retina reacts to each separate flash of a
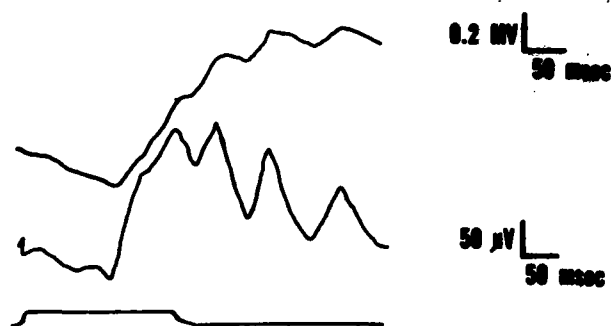
FIGURE 25. Transretinal
ERGs in response to full-
field stimulus of maximal
intensity and 200 msec
duration delivered at an
interval of 30 sec. The
top trace was recorded
with a long time constant
(T = 1 sec), and the lower
trace with a short time
constant (T = 20 msec).
(From Wachmeister and
Dowling, 1978.)
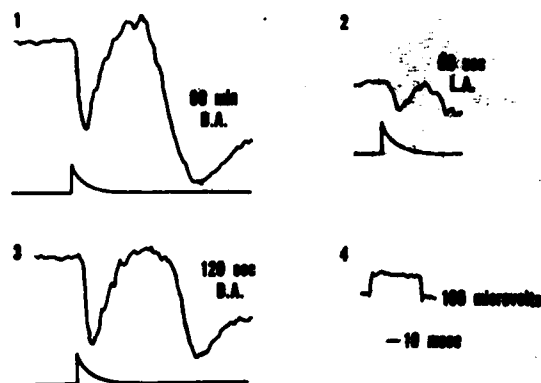
FIGURE 26. Tracings of
the electroretinograms
taken after 60 min of
dark-adaptation, 60 sec
of light-adaptation and
120 sec of dark-adapta-
tion. In all responses
the oscillatory potentials
are clearly indicated. In
these tracings the upper
trace includes the ERG,
the lower trace the event
marker. 100 µV and time
marker are indicated.
(From Genest, 1964.)
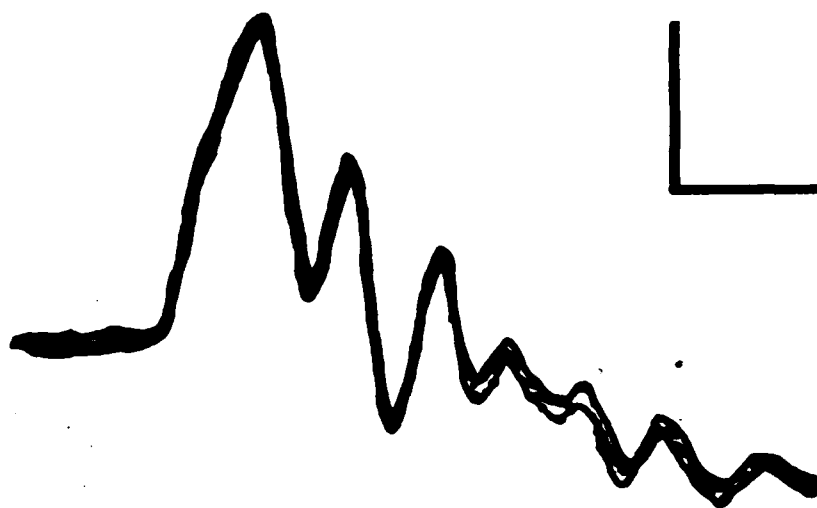
FIGURE 27. Oscillatory response of the squirrel monkey optic tract to
a light flash which starts with each trace. Three responses to the same
stimulus are superimposed. The calibration at the upper right indicates
0-3 mV vertically and 20 msec horizontally. Positivity is upwards.
(From Doty and Kimura, 1963.)

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flickering stimulus up to approximately 100 Hz (Heck, 1957), the transformation to a lower frequency must occur at a higher center.

In addition to their apparent relationship to the oscillatory potentials, the auto-oscillations may also have a tangential relationship to the proximal negative response (PNR) (Burkhardt, 1970). The PNR is a field potential generated by laterally extending amacrine cell processes. It has been noticed that the auto-oscillations are always associated with a sort of irradiation or lateral spreading of excitation. These fields appear to expand and collapse with each auto-oscillation. Although one always sees this lateral activity whenever he sees an auto-oscillation, the converse is not true, i.e., this lateral activity is sometimes seen in the absence of auto-oscillations. Also, the case in which two very strong auto-oscillations occur (double-flash effect) may be related to the dip which is sometimes seen between the photopic (x-potential) and scotopic portions of the b-wave (Figure 28, page 47).

It should be pointed out that the auto-oscillations are actually quite ubiquitous, occurring under conditions other than those described in the previous section. For example, it has been noticed during casual observation that when one has been long-adapted to room illumination and the lights are suddenly turned off, producing nearly total darkness, one sometimes sees a low amplitude fluttering which may last for several minutes. These appear to be modulations of the bleaching after-image and generally last about as long as one is aware of this after-image. A mechanical stimulus such as a hard blink sometimes helps to elicit them. The auto-oscillations previously described, on the other hand, appear to be modulations of the much shorter lasting iconic after-image. They generally continue for the duration of the iconic after-image. Thus, although approximately seven oscillations was the largest number reported for modulations of the iconic after-image, a far greater number of oscillations can be elicited when the longer-lasting bleaching after-image is being modulated.

The effects of intensity and duration are perhaps best described in terms of a physical oscillatory system. The behavior of such a system is described by the equation

$$A \frac{d^2x}{dt^2} + B \frac{dx}{dt} + Cx = F \quad \text{(Eq. 1)}$$

where in, for example, a mechanical system,

A = mass
B = resistance
C = spring modulus
x = position
and F = force

FIGURE 28. The x-, b-, and c-waves of the human electroretinogram. The lower trace shows the duration of the light stimulus. (From Motokawa and Mita, 1942.)

The response of this system can be analyzed into a natural component (due to stored or internal energy) and a forced component (due to external energy). Th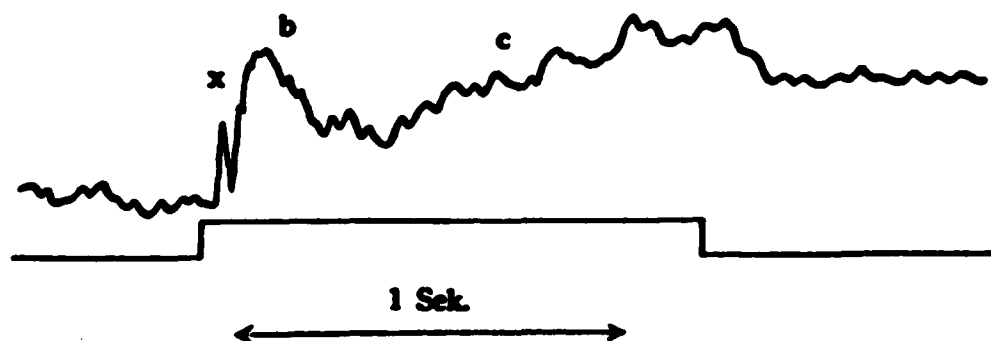e natural or transient component occurs in response to changes in the input and a comparison of the visual system's response at these points with that of the physical system is useful in highlighting some of the implications for visual theory. Such a comparison for like inputs is shown in Figure 29 (page 49). If values of A = .44, B = .04, and C = 1.24 are assigned to the physical system and a 35 msec pulse of one unit of force is delivered to it, the response is as shown in Figure 29(a) (page 49). The oscillations are due to stored energy (natural response) and the number of oscillations is determined by the resistance in the system. Figure 29(b) (page 49) is the matching pattern under Criterion I, for a 35 msec, 1.3 photopic troland, 460 nm, $1\frac{1}{2}^0$ field presented 8^0 from the fovea under conditions of a 7% recent bleach (Figure 14(b), page 30). Figure 29(c), page 49, represents an approximation to the appearance or phenomenology of the response to this pulse. The purpose of (c) is to make a more meaningful comparison to (a) by conveying an approximation to the visual system's response (since (a) is the response of the physical system) rather than simply the stimulus required to produce a match to the response as shown in (b). The actual curvatures in (c) are not known; sinusoidal waves are used only for convenience. Rather, the intent is simply to convey the fact that the observer sees smoothly rising and falling oscillations of gradually diminishing amplitude and approximately equal peak and trough durations. It can be seen that (c) is similar to (a). For the visual system, any equal-energy stimulus (all other conditions being the same) of less than about 50 msec duration produces exactly the same pattern. As duration is increased beyond this, however, the oscillations decline in amplitude. The response of the physical system to a 400 msec pulse is shown in Figure 29(d), page 49. Figure 29(e) is the stimulus pattern required to match the visual response to a 400 msec pulse with all other conditions being the same as in (b). Figure 29(f) represents the response to this pulse. Here, the visual system's response departs from that of the physical system. At the leading edge, the visual system's response shows only a half-cycle of oscillation. The extended presence of the photic stimulus suppresses the rest of the transient response. That is, in the visual system the forced response suppresses (adds resistance to) the natural response whereas in the physical system it does not. The visual system shows some oscillations at the offset of the photic stimulus but they are smaller in amplitude than those produced by a very short photic pulse. Figure 29(g) shows the physical system's response when the amplitude of the input pulse (35 msec) is increased over that which produced (a). Figure 29(h) is the matching stimulus to a 35 msec pulse whose intensity is approximately nine times greater than that in (b) and (i) is again a representation of the response. All other conditions in (g), (h), and (i) are the same as those in (a), (b), and (c), respectively. When the input to the physical system is increased in amplitude the result is an increase in the amplitude of the response and the ratio

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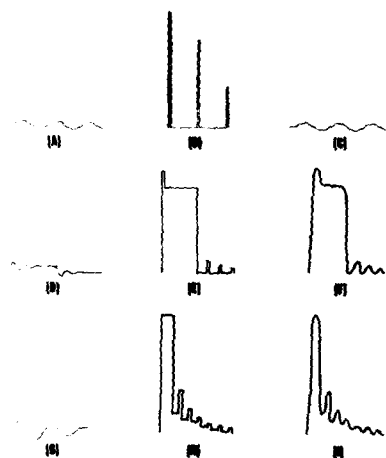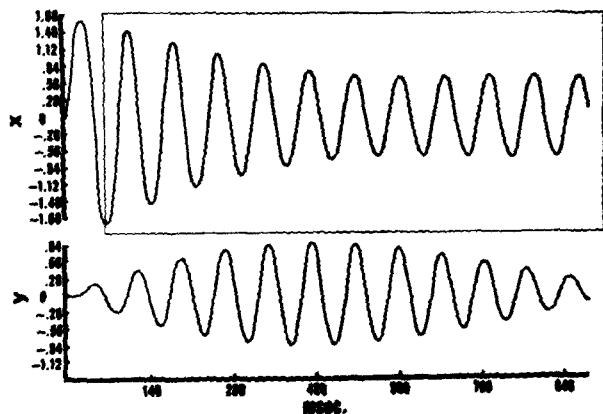FIGURE 29. See text for explanation.

FIGURE 30. The solutions to Eqs. 5 and 6 where (x) is the cone response and (y) is the rod response. In this model, the unenclosed area of the upper trace indicates the portion of the cone response that is being "read-out" by the visual system. This, followed by the rod response (lower trace) is reminiscent of the complex auto-oscillatory pattern shown in Figure 19.

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of the amplitudes for the two different inputs decreases over time if B
has a value other than zero. When the input to the visual system is
increased in intensity, however, the first oscillation "hangs-up" some-
what, i.e., there is a long-duration peak, and the subsequent oscilla-
tions are reduced in amplitude. The changed form of the visual system's
response produced by increasing the amplitude or extending the duration
of the input pulse can be accommodated by the oscillatory equation if
the B coefficient is changed from a constant to some function $(G(i))$ of
the intensity of the input. For example, the high intensity input whose
response pattern is shown in Figure 29 (i), page 49, would produce a
sharp increase in the resistance (G) coefficient which would cause the
first peak to "hang-up." Eventually, oscillation would resume but at a
relatively low amplitude due to the fact that the initial increase in
resistance resulted in less energy being stored in the system. In the
case of the extended duration input and its associated response (F), the
extended presence of this input would suppress most oscillatory activity
at its onset. At its offset, however, oscillatory activity would resume
but, again, at a relatively low level. Thus, the equation now becomes

$$A \frac{d^2x}{dt^2} + G \frac{dx}{dt} + Cx = F. \quad (Eq. 2)$$

Equation 2 would seem to be a fairly good descriptor of the response
to a 460 nm pulse presented 8^0 from the fovea where, under the adapta-
tional conditions considered, the response is primarily from the rods.
Under conditions where there is a stronger cone contribution and, pre-
sumably, a more intense rod-cone interaction, a somewhat more complex
model seems to be required. Figure 10, page 25, shows that, relative
to the vast differences in photopic brightness among the three chroma-
ticities, their two-population peaks are fairly close to each other in
terms of scotopic brightness. As pointed out earlier, this, however,
does not mean that the oscillations are solely rod-determined since the
peaks are at different heights for the different chromaticities. What
is the nature of the rod-cone interaction in these oscillations? It
will be argued here that it bears some resemblance to the behavior of a
pair of coupled oscillators. This type of system is described by two
simultaneous equations:

$$A_c \frac{d^2x}{dt^2} + M \frac{d^2y}{dt^2} + B_c \frac{dx}{dt} + C_c x = F_c \quad (Eq. 3)$$

$$A_r \frac{d^2y}{dt^2} + M \frac{d^2x}{dt^2} + B_r \frac{dy}{dt} + C_r y = F_r \quad (Eq. 4)$$

Where Eq. 3 represents the cone behavior, Eq. 4 represents the rod
behavior, and M is the degree of coupling between the two systems. It

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is hypothesized that the initial cone generated response, which occurs first, partially blocks the initial rod-generated response. This impedance results in stored energy in the rod-generated response producing a rebounding effect which increases the strength of the auto-oscillations. In a physical coupled oscillation system this impedance and enervation is part of a continuous energy transfer from one system to the other. As Figure 10 (page 25) shows, the 555 nm stimulus which would be expected to produce approximately equal rod and cone responses under these adaptation and retinal locus conditions produces the strongest two-population oscillations. When the cone contribution is either increased (620 nm stimulus) or decreased (460 nm stimulus), while the rod contribution is held relatively constant, the auto-oscillations become weaker. This is analogous to the fact that in a physical coupled oscillation system the maximum power transfer occurs when the two systems have equal impedances. If the intensity is too high or the pulse duration too long, the oscillations at this 2^0 locus are largely suppressed just as was shown for the 8^0 locus. Therefore, as in Eq. 2, the coefficients of the first order terms are made functions and the equations now become

$$A_c \frac{d^2x}{dt^2} + M \frac{d^2y}{dt^2} + G_c \frac{dx}{dt} + C_c x = F_c \quad \text{(Eq. 5)}$$

$$A_r \frac{d^2y}{dt^2} + M \frac{d^2x}{dt^2} + G_r \frac{dy}{dt} + C_r y = F_r \quad \text{(Eq. 6)}$$

with Eq. 5 representing the cone-generated response and Eq. 6 representing the rod-generated response. Figure 30 (page 49) shows the solutions for the cone-generated response $(30(x))$ and the rod-generated response $(30(y))$ when values of $A_c = .94$, $G_c = .07$, $C_c = 6.63$, $A_r = .69$, $G_r = .03$, $C_r = 10.83$, $M = .04$, $F_c = 1$ and $F_r = .05$ are substituted into the equations. The initial conditions are $x = 0$ and $y = 0$. Under these intensity and adaptation conditions, constants can be used to approximate G_c and G_r.

If the visual system first "reads-out" the initial response (unenclosed area) of the shorter-latency cone system and then the longer-latency rod response, the overall response bears some similarity to the complex pattern depicted in Figure 19 (page 35). That is, there is an initial large cone response followed by some rod oscillations which increase in amplitude and then diminish. The enclosed area, while not being directly "read-out" is, of course, directly interacting with that which is being "read-out."

In an interesting tangential observation, we found what could be called a case of rod-cone silent substitution. We noticed when a long-wavelength pulse is used to excite rods and cones approximately equally (Figure 31, page 54) under conditions of full or nearly full dark adaptation, one sees two distinct parts to the response. For example, when

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a 35 msec, 20 photophic troland, 680 nm test pulse of $1\frac{1}{2}^0$ diameter was presented 8^0 from the fovea with the eye at an approximately 2% rhodopsin bleach and 0% chlorolabe and erythrolabe bleach, the observers first saw a chromatic response apparently produced by the shorter-latency cones and then an achromatic response apparently produced by the longer-latency rods. In terms of luminance, the two responses appeared equal and the first response blended smoothly into the second one such that there was no transient between them (Figure 32, page 55).

This would seem to constitute observational evidence for McLeod's (1972) belief that the steady field which he produced at mesopic levels was due to the fact that the rod and cone responses are out of phase. He presented, 5^0 above the fixation point, a yellow flickering test patch superimposed on a blue-green background and found that at 7.5 Hz the flicker was clearly observable at scotopic and photopic test patch intensities but appeared steady at mesopic levels. That is, at mesopic levels and with a moderately short-wavelength background to suppress the rod response more than the cone response, one would expect the area of superimposition of the two curves in Figure 1 to shift somewhat to the left such that a yellow stimulus might excite rods and cones approximately equally. If such a pulse first produced a response from the shorter-latency cones and then a response of approximately equal magnitude from the longer-latency rods, the rod response would substitute silently for the cone response. Furthermore, if a second pulse were presented at the right interval the initial cone response would substitute silently for the preceding rod response and so on, thus producing a field which appeared steady.

The results of an electrophysiological study by Gouras and Link (1966) in which they recorded from retinal ganglion cells in the Rhesus monkey are of interest in this connection. They used a long-wavelength stimulus which, under their conditions, excited primarily cones and a short-wavelength stimulus which excited primarily rods* and presented these stimuli in various temporal relationships. When stimulus intensities which produced approximately equal rod and cone responses were used, it was found that whichever response arrived first at the ganglion

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* It will be noted that the stimuli used by Gouras and Link to excite rods and cones equally differed from ours in that ours did not include a short-wavelength component. If the spectral response functions of the rods and cones of the two species are similar, their need for a short-wavelength stimulus would indicate that their preparation was held at a somewhat higher state of light adaptation than were our human subjects.

cell blocked the other one. In the case where the rod and cone stimuli were presented at the same time, the shorter-latency cone response cancelled the rod response. The psychophysical findings suggest that such a cancellation does occur in phasic units.* That is, the second, silently-substituted response would not be expected to produce a phasic signal. On the other hand, the psychophysics suggests that a cancellation of this sort does not occur in tonic units.

CONCLUSIONS

Under a wide range of adaptational conditions and stimulus pulse intensities the human visual system has an inherent tendency to oscillate upon being stimulated by a brief photic pulse.

Although these oscillations are stronger when both the rod and cone populations are involved, they also occur when only a single population is stimulated.

These oscillations would seem to be closely related to those observed in the electroretinograms of humans and other species.

These perceptual oscillations can be mistaken for equipment malfunctions in Army aircraft lighting equipment which generates short photic pulses.

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* That they were recording from phasic units has since been confirmed by Gouras (personal communication).

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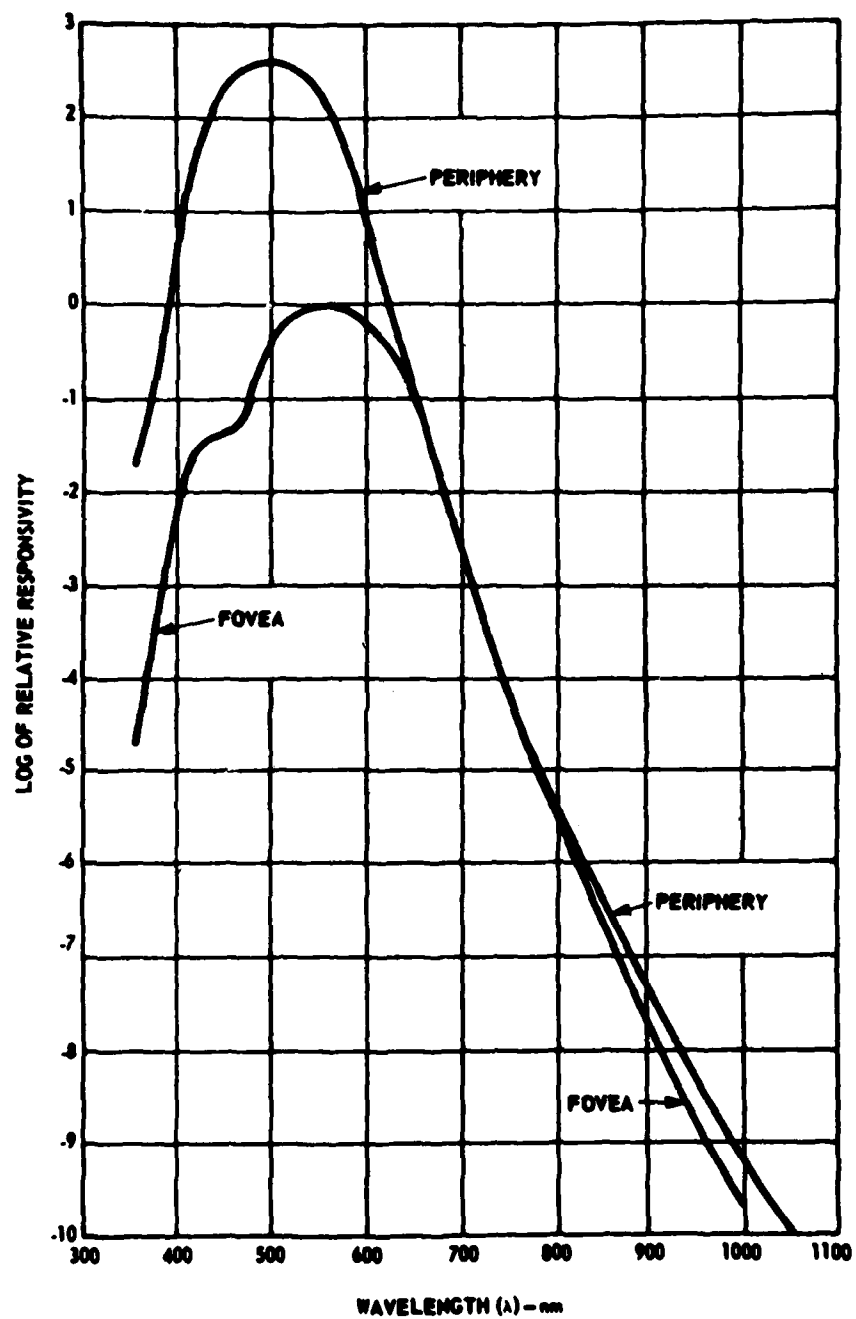
FIGURE 31. Relative spectral responsivity of the dark-adapted fovea and peripheral retina (adapted from Griffin et al, 1947).

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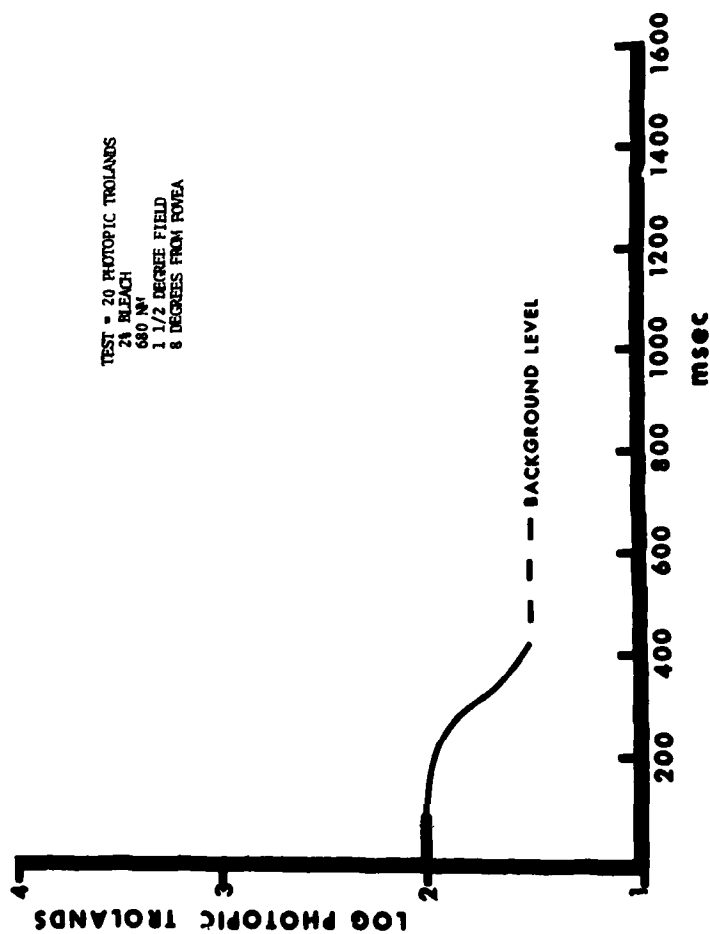
FIGURE 32. The match to a 20 photopic troland, 680 nm, 1½° stimulus presented 8° from the fovea under conditions of a 2% rhodopsin bleach. The wide line represents the approximate duration of the chromatic (red) portion of the response and the narrow line represents the achromatic portion of the response.

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